

USING DISPERSAL RATES TO GUIDE TRANSLOCATION ACROSS IMPERMEABLE WILDLIFE RESERVE BOUNDARIES: HAWAIIAN TREE SNAILS AS A PRACTICAL EXAMPLE

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ABSTRACT

Discontinuous wildlife reserves can lead to inbreeding depression for fragmented populations of threatened species. To offset such effects, conservation managers frequently turn to translocation strategies, such as the one-migrant-per-generation rule (OMPG), which relies on many unrealistic assumptions of Wright's (1931) island model. We therefore propose an alternate translocation approach based on the natural dispersal rates of focal species, using two endangered Hawaiian tree snails species, *Achatinella sowerbyana* and *A. mustelina*, as practical examples. The rate at which tree snails historically dispersed across reserve boundaries can be used to guide contemporary translocation across those dispersal barriers. Snail movements were monitored for three years using capture-mark-recapture (CMR) methods, and analyzed with a multi-strata model in program MARK to obtain survival and dispersal rates. We tested and ranked models, including age, time, weather, and location effects on survival, dispersal, and capture probabilities. Annual mortality ranged from over 50% to less than 20%, by site, mirroring expectations from anecdotal observations of predator abundances. Monthly dispersal rates between isolated tree clusters were recorded between 3% and 24% of a population, depending on the population's exposure to severe weather rather than its species designation. Simulations based on dispersal-distance distributions were then applied to estimate emigration rates beyond the finite study sites. Emigration rates ranged among sites from 0.7% to 6.7% of the population per month, translating to between 6 and > 100 emigrants per year, depending on the density of snails at each site and the site's dimensions. The site boundaries are directly analogous to current and future reserve designs, and we show how such emigration rates can be used to guide two-way translocation rates across such artificial barriers.

Key words: *Achatinella*, OMPG, Program MARK, CMR, conservation.

INTRODUCTION

Across the globe, habitat loss and other anthropogenic causes have led to a drastic decline in biodiversity over the past century (IUCN, 2009). Many formerly vast and continuous ranges of animal species have been reduced to patches of fragmented habitat. The most common and intuitive conservation approach involves protecting the survivors' remnant natural habitat through reserve designations. Often, however, these reserve systems comprise only a fragmented landscape of former species distributions, with no means of natural connectivity among them.

All but the most vagile of species are restricted to mating only with other individuals within such isolated reserves. While not especially problematic in large populations, individuals in smaller threatened populations are forced to mate with relatively closer relatives by default, or might even avoid mating entirely (Ingvarsson, 2002). For species that normally outbreed with distinctly non-related members of the population, this can have dire consequences. Inbreeding depression, the reduced fitness resulting from breeding of closely related individuals, is a major concern when managing the survival of any small and threatened population (Leberg, 1990).

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To mitigate mating avoidance and inbreeding depression effects, as well as to prevent artificial divergence among fragmented subpopulations, conservation managers often advocate the reestablishment of migration corridors (Beier & Noss, 1998). However, logistical constraints, such as urbanization (e.g., roads forming barriers and land use changes), often preclude the feasibility of establishing such corridors for many species. Those species are then prime candidates for translocation. This strategy involves the human-assisted movement of individuals between reserves to restore some level of historical and natural connectivity.

The one-migrant-per-generation (OMPG) rule (Mills & Allendorf, 1996) is still the most common guideline for translocations in conservation management. However, OMPG is based on many unrealistic assumptions, such as Wright's (1931) island model, which assumes that natural migration is equally likely between any pair of populations regardless of the distance between them. This suggests that each migration event provides recipient populations with a random genetic sample of the entire species.

Few species actually fit this pattern, because migration between nearest neighbor populations is much more common for most species. A migrant from a closely related neighbor population would thus have a substantially lower effect at overall species homogenization than would a distantly related migrant from across the species' range (Mills & Allendorf, 1996). In light of this, more migrants than OMPG may be necessary from local neighbor populations if one is to mimic natural migration, prevent the divergence of populations, and reduce inbreeding concerns (Mills & Allendorf, 1996).

We discuss only translocation among neighboring populations in this paper, because the consequences of excessive outbreeding from distantly related populations could be equally detrimental to species survival (Edmands, 2007). To employ some modification of OMPG using neighbor populations, one would first need to address a difficult question: how many migrants from neighboring geographic sources would provide the equivalent amount of new alleles to an inbred population, as would a single random migrant sampled from the entire species? We instead suggest an alternative translocation approach that mimics the historical levels of gene flow that a migration corridor would have provided. If the natural migration

patterns of a species can be approximated, it may be possible to artificially mimic historical connectivity among now-fragmented populations.

The entire pulmonate genus *Achatinella*, endemic to the island of O'ahu, Hawai'i, is listed as "critically endangered" (IUCN, 2009). Several remnant species exist as recently fragmented populations in need of translocation. We use these snails to demonstrate a real-world practical application of our approach. The main contemporary threat to these species' survival is from invasive predators, and efforts to create protected snail reserves are already underway (Hadfield et al., 2004). Two *Achatinella* spp. populations have already received predator-proof enclosure fences for *in situ* preservation, with more planned in the coming years.

However, the impermeable nature of these enclosures leaves open the possibility of excessive inbreeding that could ultimately reverse any progress towards protecting these snails. Without a translocation strategy, confining snails to enclosures further restricts gene flow among these already severely fragmented populations. However, if following the erection of a fence there are still individuals in the vicinity of the fenced-off area, then localized translocation is still possible.

Preliminary studies have revealed that these strictly arboreal snails disperse primarily by being blown off of trees by strong wind gusts, then climbing up the nearest vegetation (Hall & Hadfield, 2009). We investigated the rate at which this migration occurs by monitoring two *Achatinella* spp. using capture-mark-recapture (CMR) techniques. Although assessing dispersal rates was our primary objective, our analyses also accounted for variation in recapture and survival probabilities to reduce bias in our estimated dispersal rates. Resultant survival rates could further be used to assess the immediacy of threats to populations, and to prioritize conservation initiatives.

Achatinella mustelina Mighels, 1845, and *A. sowerbyana* Pfeiffer, 1855, were selected for this study because they are both relatively abundant and represent opposite extremes of the genus with regards to climate (Hall & Hadfield, 2009) and evolutionary history (Holland & Hadfield, 2004). It was thus hoped that any resulting similarities might be applicable to conservation efforts for all species in this genus. Our data provided a basis for estimating emigration across potential reserve boundaries, and for guiding rates of future translocation.

METHODS

Data Collection

Two replicate sites were selected for each species and are located at the extreme north/south ends of the known species ranges to further account for any climatic variation (Fig. 1). These are Palikea (Nature Conservancy Hono'uli'uli Preserve) and Kahanahāiki (Makua Military Reservation) in the Wai'anae Mountains for *A. mustelina* (18 km apart), and north of the Poamoho monument (Ko'olau Summit Trail (KST)) and west of 'Ōpae'ula Cabin (Army leased land, west of the KST) in the Ko'olau Mountains for *A. sowerbyana* (2 km apart). A grid of quadrats, each 2.5 m x 2.5 m, was laid out covering the entire area within a site's boundaries (each site enclosing < 1,500 m²). The number of quadrats varied substantially among sites due to local terrain; steep cliffs were present in some sites that were unsafe to survey (Fig. 2).

Surveys to monitor snail dispersal were conducted at each site from late 2005 (month varied by site) to August 2008. Intervals between surveys were roughly three months, although with some variability. In total, nine surveys were completed at 'Ōpae'ula, ten at both Palikea and Poamoho, and 12 at Kahanahāiki. Surveys were conducted on single-day trips by two observers, and 3–5 minutes were devoted to each quadrat (more time was devoted to quadrats with higher density vegetation). A final survey at each site was conducted over the course of two

days in August 2008, involving four observers to maximize long-term dispersal detection. This increase in snail sighting probability for the final survey was accounted for in the analyses.

All surveys involved recording location data of recaptured snails and marking new ones. Dispersal was measured as the distance between the centers of trees, with "trees" also referring to clusters of trees with overlapping branches (rarely > 5 m² at any site). Snails can freely disperse between such connected trees, and our focus was on the wind-dispersed movements between unconnected trees.

Capture-Mark-Recapture

Every snail found was measured (shell length and width) and labeled with a unique code upon first capture. Snails with shells over 7 mm in length were alpha-numerically marked using letters and numbers printed on paper punch-outs (one for the letter and one for the number). Six-point font characters were printed onto waterproof paper (Rite-In-The-Rain), and cut out with a leather punch. In the field, the snail's shell was gently dried and cleaned, and then a small drop of cyanoacrylic glue (Satellite City "Super T") was applied to it. The two punch-outs were then placed onto the glue, followed by another drop of the transparent glue to protect the marks from deterioration. When the glue had dried, the snail was returned to its capture location. Subsequent recaptures were only sightings, and further handling of the snail was unnecessary.

The punch-out method of marking (Barry Smith, University of Guam) we used resulted in a very low tag-loss rate (< 0.01 per month), which is necessary to avoid biased parameter estimates (Henry & Jarne, 2007). These tags are also functionally identical to the plastic tags that proved most resistant to deterioration in a comparative study of different snail marking methods (Henry & Jarne, 2007). Tag-loss was recorded as snails showing either only residual glue on their shells or having only one punch-out present. With moderate recapture rates and low dispersal, it was usually possible to deduce the identity of individuals with missing tags at a later date by looking at the encounter histories of other snails.

Although Henry & Jarne (2007) highlighted the deterioration risks of using different colored paint dots, individual color-codes last at least one year in field studies (K. Hall, personal observation). Snails less than 7 mm in length

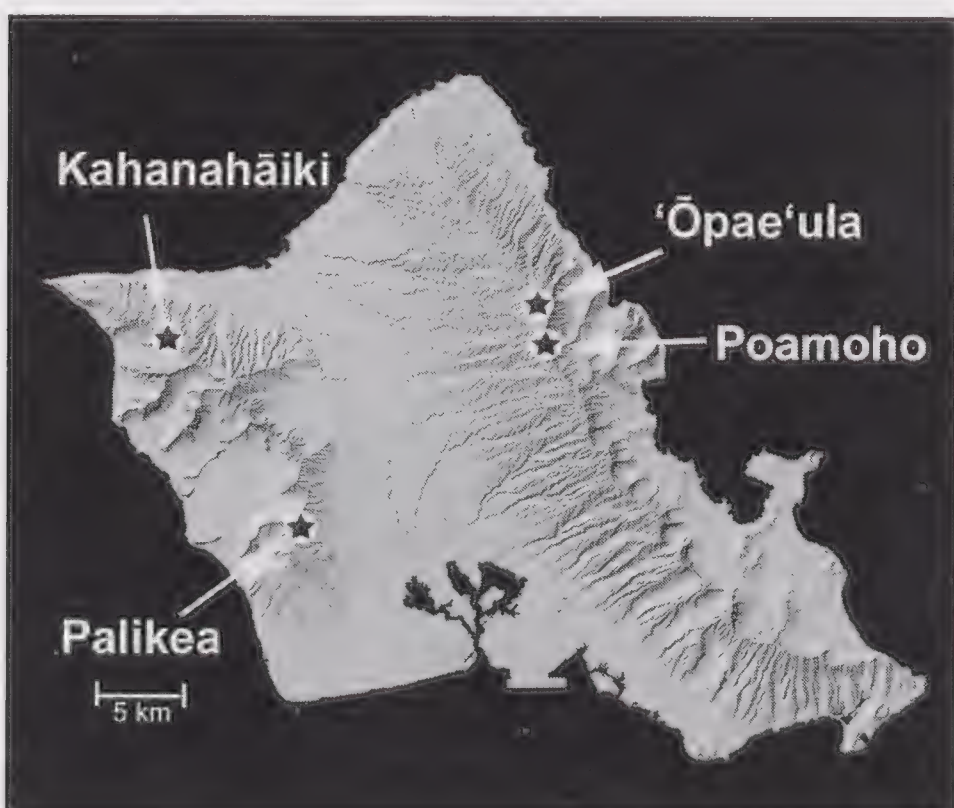


FIG. 1. The island of O'ahu. Points mark all four field site locations (courtesy of State of Hawai'i, Office of Planning).

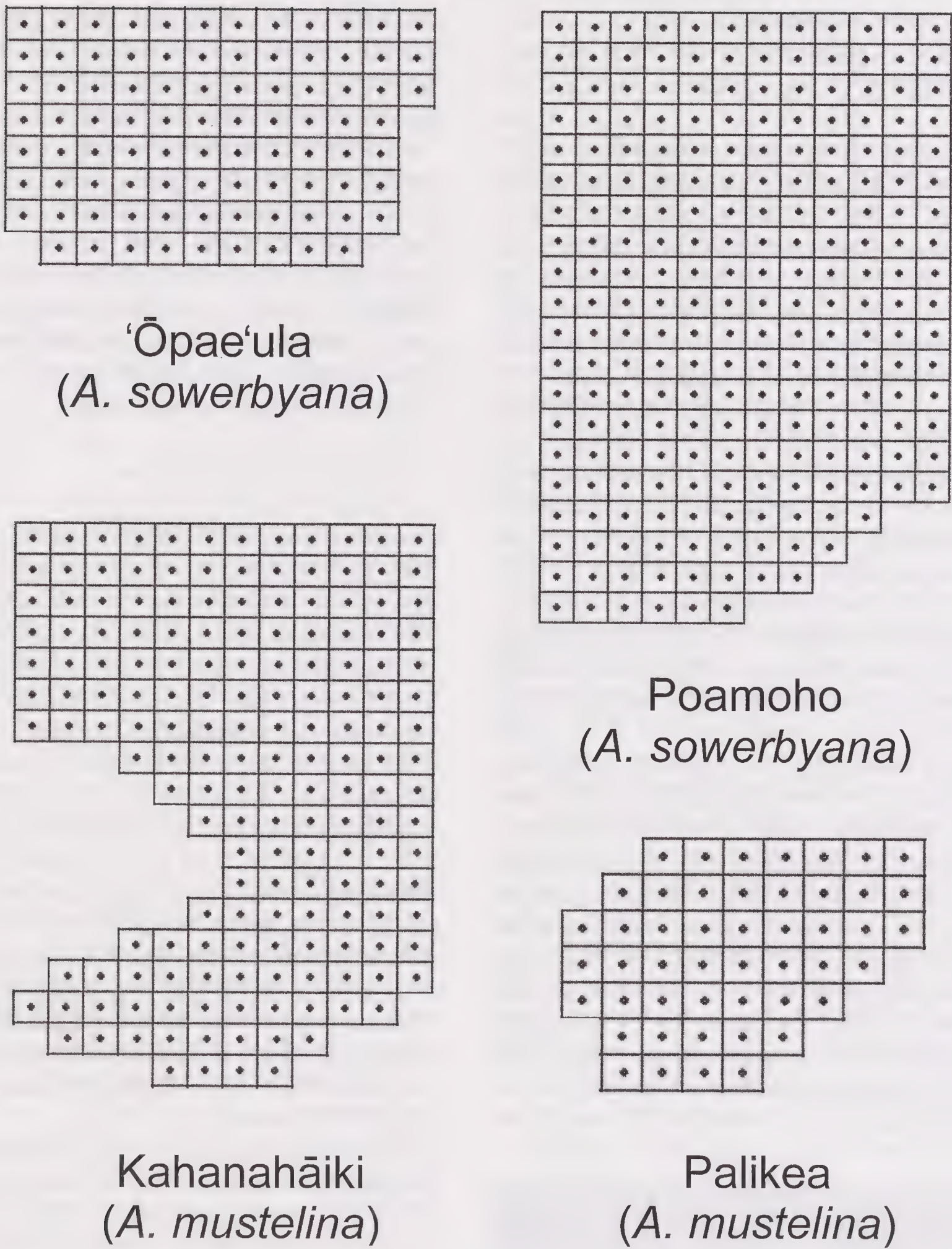


FIG. 2. Grid maps of the 4 sites used in this study. Each square quadrat represents 6.25 m².

received small circular dots using paint pens until they grew large enough to receive the paper marks. Using growth rate estimates (Hadfield et al., 1993) this can occur in less than one year even for the smallest sizes of juvenile snails.

Analysis of CMR Data

Model Structure – Each site was analyzed independently using a multi-strata design in Program MARK (White & Burnham, 1999)

to obtain simultaneous estimates of survival (ϕ), probability of capture (p), and probability of dispersal (ψ) parameters. To use Program MARK, one first needs to construct a global model. For each parameter, this linear model includes all variables under consideration that may have a significant effect on that parameter, including interactions. Reductions of the global model are then constructed based on plausible biological hypotheses, and reduced models are subsequently ranked to determine which hypotheses are best supported by the data.

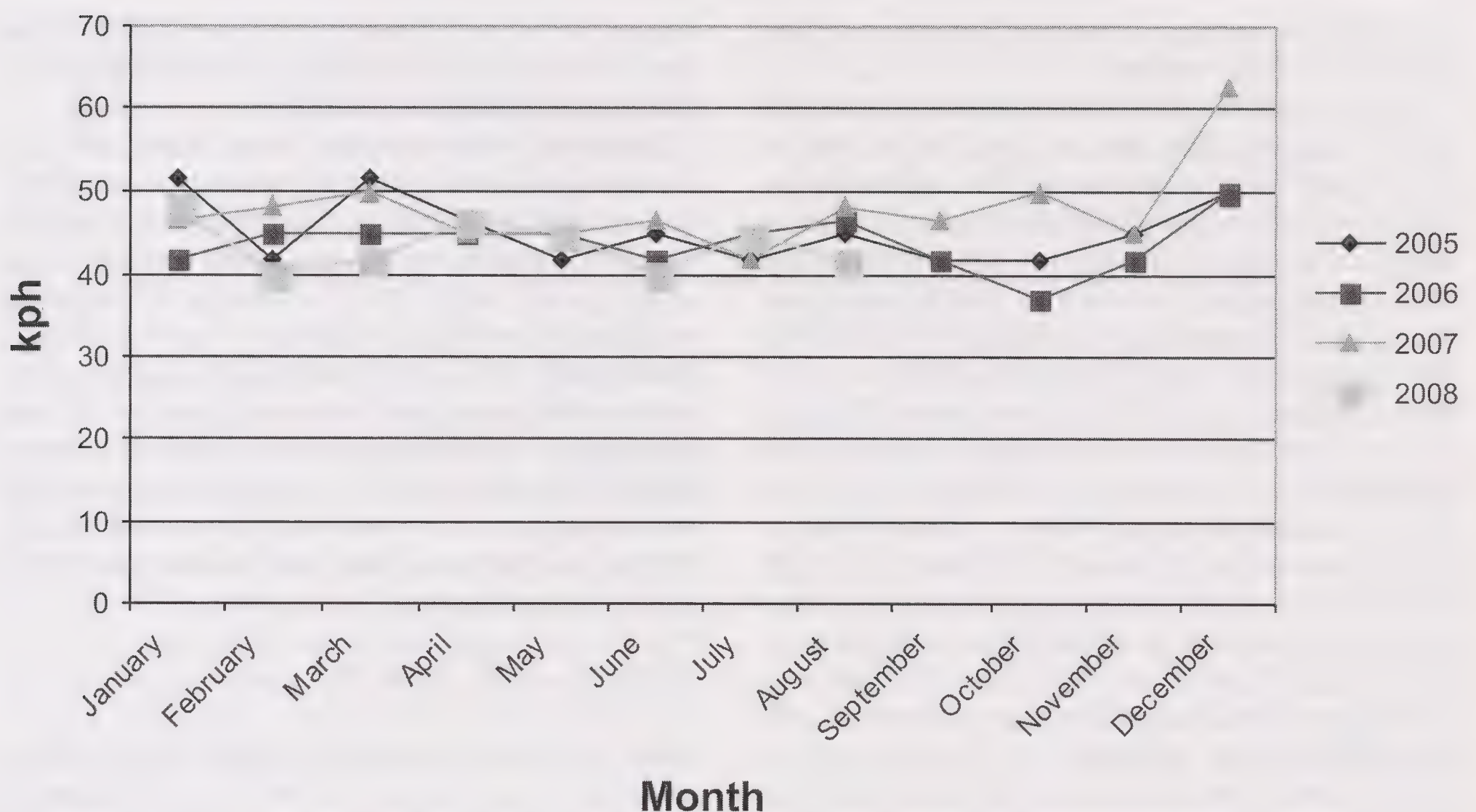


FIG. 3. Maximum monthly wind speed at HNL airport from January 2005 through August 2008.

An example of a reduced model using the conventional model notation (Lebreton et al., 1992) is $\phi(c)p(t*s)\psi(\cdot)$, which means that survival (ϕ) was allowed to vary by variable c , capture probability (p) was allowed to vary by variables t and s (and their interaction), and dispersal (ψ) was constrained to a single parameter estimate. Full reduction of a parameter (no variation) is represented by $\phi(\cdot)$, $p(\cdot)$, or $\psi(\cdot)$, with the most reduced model possible (only three estimated parameters) being $\phi(\cdot)p(\cdot)\psi(\cdot)$.

The typical capture-history notation for multi-strata models uses letters to represent different locations (A, B, C, etc.) where an animal could be at a given time, and the model output is a series of ψ parameters to estimate the probability of transition between each pair of strata (locations) over a given time interval. We only estimated a *generic* dispersal parameter for each time interval (Zimmerman et al., 2007), because specific tree combinations were unimportant for calculating dispersal rates. These rates reflect the frequency that dispersal occurs; *distances* of such movements were analyzed separately.

Model Variables – Age was hypothesized to influence ϕ , p , and ψ . Three age-classes were designated, based on previous studies of *Achatinella* spp. that showed varying survival

between juveniles (0–1 years), subadults (1–2 years), and adults (2+ years) (Hadfield et al., 1993). Using growth measurements and modified logistic growth curves (Kaufmann, 1981; Hadfield et al., 1993), we assigned all snails in our study to one of these three age-classes at each time interval regardless of whether they were captured. A model containing $\phi(a)$, $p(a)$, or $\psi(a)$ would simply mean that survival, capture, or transition probability was allowed to vary among these three age categories in that model ($\phi(a)$ means three ϕ parameters were estimated, one for each age-class). Age-classes were also combined to reduce the number of parameters in some models, such as $\phi(\text{juv/non})$, which constrains ϕ to a juvenile (1st year) estimate and an “all other ages” estimate.

Temporal influence was suspected in survival and capture probabilities, which are represented by the $\phi(t)$ and $p(t)$ model notations, respectively (8–11 ϕ or p parameters estimated, according to the number of between-survey intervals at each site). Transition probability was only allowed to vary with time around the December 2007 interval (model notation $\psi(\text{dec07})$), when the highest winds between 2005 and 2008 were recorded (United States Weather Bureau, 2008) (Fig. 3). Based on Hall & Hadfield’s (2009) suggestion of a wind-dispersal mechanism for *Achatinella* spp., we assumed that if any major wind influence on ψ

would be detectable, it would be following the December 2007 storm.

Tree location (stratum) was not expected to have any effect on survival or transition probability. Since we were only estimating a single generic movement parameter, our three different strata (A, B and C) only represented “same tree as last survey”, “dispersal to flagged tree”, and “dispersal to un-flagged tree”. This last distinction was to address a known bias in recapture probability; trees were flagged in the field for reference when snails were captured, but snails have a strong preference to rest subsequently on flagging tape. Thus, a single tree could represent both strata A and B at the same time (and maybe C in a previous interval) – letters merely denote whether or not a snail had moved and the presence/absence of flagging. However, since C represents a tree without flagging, differences in capture probabilities were anticipated from those of A or B (previously flagged trees). Models with $p(s)$ denote that capture probability was allowed to vary between 2 groups (C and A+B); no models contained $\phi(s)$ or $\psi(s)$.

Model Selection and Parameter Estimation – A set of candidate models was created to compare varying hypotheses, each testing various combinations of variables on our three parameters of interest (ϕ , p , and ψ). All models tested were reductions of that site’s global model, as is required for such comparisons. Based on the variable descriptions above, the global models’ structures included interactions among all age-class categories (juvenile, subadult, adult) and between eight and eleven survey intervals (depending on the site) for ϕ ; age-class, strata, and time interval for p ; and age and weather for ψ . Program MARK uses Akaike’s Information Criterion (AIC – Akaike, 1974) to then rank reduced models by their relative likelihoods, and determine which model structures are most supported by the data provided.

To account for any overdispersion in our data, we tested the goodness of fit for our global models first. We chose the median c-hat approach implemented in Program MARK, which is the most appropriate test when the global model is not fully time dependent (Cooch & White, 2007: 5–29). The resulting variance inflation factor (c-hat) was used to adjust the model rankings in Program MARK. Model rankings that are adjusted for c-hat and sample sizes are denoted by QAICc (quasi-likelihood)

rather than AIC (Cooch & White, 2007). The top ranking models at each site correspond to the lowest QAICc values.

Dispersal and survival rates were not obtained directly from the top model (lowest QAICc), since no site’s top model received more than 75% support relative to other models. This support was measured by the w_i ’s (the Akaike weights, normalized so they sum to 1 for the model set). Uncertainty in model selection was addressed using a technique known as “model averaging” (Anderson, 2008) within Program MARK. Model averaging weighs each model according to its w_i , then provides a single estimate for the parameter and associated 95% confidence interval.

Emigration Simulation

To estimate emigration rates, we used a simulation technique that had been used previously with birds (Baker et al., 1995; Sharp et al., 2008). Limitations of such methods can be substantial for highly mobile species (Koenig et al., 2002), which tree snails are not. We first corrected our observed dispersal distance distributions for those dispersal events we missed due to emigration. This was done by simulating the entire range of observed dispersal distances from each quadrat in all directions, and then determining the proportion of simulated post-dispersal positions that occurred outside the boundaries of the site.

For each dispersal distance (in one-meter intervals), we used the ratio of off-site/on-site post-dispersal positions to provide a less biased frequency of that distance. As an example, if during simulation, 50% of all ten-meter dispersal events resulted in positions off-site, then we would have underestimated the frequency of ten-meter dispersers during our field studies by 50%. Thus, if we had observed eight ten-meter dispersers during field studies, the corrected frequency would now be 12 (= eight observations + 50% underestimate correction).

We then reran the simulations (50,000 iterations) using the corrected dispersal distributions, to again determine the proportion of all simulated post-dispersal positions that occurred outside the boundaries of each site. Proportions were calculated for every quadrat within the grids (Fig. 2). Values from all quadrats were then averaged to obtain a single proportion for each site. These proportions allowed us to estimate emigration rates. We assumed that we underestimated our uncorrected dispersal

rates (obtained using Program MARK) by an amount equivalent to these off-site proportions. Emigration was calculated by multiplying the off-site dispersal proportion by the uncorrected dispersal rate. For instance, a site with an average simulated off-site proportion of 40% and an uncorrected dispersal rate of 10% would have an emigration rate of 4% (40% x 10%).

Accounting for emigration allowed us to reduce bias in our original estimates of dispersal and survival. Corrected dispersal rates were obtained by adding the emigration rate directly to the original, uncorrected dispersal rate. Our original survival estimates also suffered from underestimation by not addressing emigration. To obtain less biased estimates of survival, we re-reran our MARK analyses including a fourth transitional stratum, U , which was set equal to the emigration rate of the site. Corrected estimates of survival were obtained from these models.

Application to Management

Calculating a suitable number of immigrants and emigrants for active conservation management requires knowing the density of the population, the dimensions of the proposed or existing reserve, and the average level of emigration expected from a reserve of those dimensions. Estimates of abundance were obtained by utilizing the Lincoln-Peterson estimator (Chao & Huggins, 2005). As described in the "Data Collection" section, an intensive survey was conducted at each site on one day, followed by a repeat of the same survey on the following day. This allows these nocturnal snails to re-mix within their host trees (< 3 m in height) overnight (Hall & Hadfield, 2009). By multiplying the reserve's simulated emigration rate (percent of population per month) by the number of animals present (population density x reserve dimensions), one can approximate the historical level of gene flow across the reserve boundaries. An example using data from Palikea is discussed to illustrate this application.

RESULTS

Model Averaging and Parameter Estimates

Goodness-of-fit tests (using median c -hat procedures) indicated that the global models provided adequate fits to the data with minimal

overdispersion. C -hat adjustments of 1.19, 0.98, 1.18 and 1.35 were made to 'Ōpae'ula, Poamoho, Kahanahāiki, and Palikea, respectively, before model selection began. These adjustments inflate sampling variances, which leads to a lower risk of falsely identifying a factor as important in a model. Table 1 shows the model rankings for each site based on QAICc criteria; top models are those with the lowest QAICc. Only the top four models at each site are presented, which includes all models with at least 10% support according to w_i 's.

For sites where age-varying models of survival were among the top two models ('Ōpae'ula and Kahanahāiki), model averaging was used to provide age-specific survival rates; otherwise a single survival parameter was estimated (Table 2). Also included in Table 2 are the corrected estimates of survival obtained by incorporating emigration; most estimates show significant increases as expected. Those estimates that showed decreases were both juvenile estimates, which already suffered from large standard errors and are unreliable.

Detection probabilities varied temporally (two-person surveys vs. the final four-person survey) at all sites except Palikea, which has nearly 75% less area included in the study grids making it easier to survey. Additional effort thus had little effect on the already high capture rates. Detection also varied with age and strata at two sites each (Table 1). At these sites, older (larger) snails and individuals in flagged trees were recaptured more often. More than 20 p parameters were estimated because of interactions among variables in top models; differences in sites' recapture rates are thus more easily displayed by analyzing raw data. Over 1,000 snails were captured and marked (394 at 'Ōpae'ula; 124 at Palikea, 226 at Poamoho, and 314 at Kahanahāiki). The average number of times a snail was recaptured was 0.95 ± 1.06 , 1.31 ± 1.92 , 0.79 ± 1.07 , and 1.23 ± 1.88 , in the same order. Both *A. mustelina* populations had the highest recapture rates; a frequency distribution of individual recaptures is provided in Figure 4.

Dispersal increases were detected after the December 2007 storm at every site in at least the 2nd best model, including the best model for Poamoho (Table 1). These dispersal rate estimates (percent of snails dispersing per month) are provided in Table 3. Distributions of observed (uncorrected) dispersal distances are shown in Figure 5, most were less than 10 m. Longer distances (> 20 m) were recorded

TABLE 1. Top four models at each site, ranked according to QAICc values. Δ QAICc is the difference in QAICc from top model, w_i denotes Akaike weight, Np is the number of estimable parameters in each model, and QDeviance (a major determinant of QAIC) is each model’s deviance after adjusting for overdispersion.

Species	Site	Model	QAICc	Δ QAICc	w_i	Np	QDeviance
<i>Achatinella sowerbyana</i>	Poamoho	$\varphi(.)p(t)\psi(\text{dec07})$	956.33	0	0.74	6	429.91
		$\varphi(.)p(t)\psi(.)$	959.63	3.29	0.14	5	435.29
		$\varphi(.)p(t)\psi(a)$	961.21	4.88	0.06	6	434.79
		$\varphi(\text{adult/non})p(t)\psi(.)$	961.59	5.26	0.05	6	435.17
	'Ōpae'ula	$\varphi(a)p(t^*s)\psi(.)$	1,293.98	0	0.48	10	505.60
		$\varphi(a)p(t^*s)\psi(\text{dec07})$	1,295.09	1.11	0.27	11	504.60
		$\varphi(.)p(t^*s)\psi(.)$	1,295.74	1.77	0.20	8	511.55
		$\varphi(a^*t)p(a^*t^*s)\psi(\text{dec07})$	1,298.77	4.79	0.04	24	479.84
	Palikea	$\varphi(.)p(a^*s)\psi(.)$	562.49	0	0.37	8	343.00
		$\varphi(.)p(a^*s)\psi(\text{dec07})$	563.56	1.08	0.21	9	341.92
		$\varphi(\text{adult/non})p(a^*s)\psi(.)$	564.12	1.63	0.16	9	342.48
		$\varphi(\text{juv/non})p(a^*s)\psi(.)$	564.55	2.06	0.13	9	342.91
	Kahanahāiki	$\varphi(\text{juv/non})p(a^*t)\psi(.)$	1,648.62	0	0.33	12	821.78
		$\varphi(\text{juv/non})p(a^*t)\psi(\text{dec07})$	1,650.05	1.43	0.16	13	821.11
		$\varphi(.)p(a^*t)\psi(.)$	1,650.22	1.59	0.15	11	825.45
		$\varphi(a)p(a^*t)\psi(.)$	1,650.49	1.87	0.13	13	821.56

at all sites except Palikea, which is smaller in area. Regression analyses of the relationship between dispersal interval (days between observations) and distance traveled indicate that longer movements are not exclusively sums of successive shorter movements. R^2 values were 0.2% ($p = 0.76$), 34% ($p = .01$), 0.7% ($p = 0.76$), and 1% ($p = 0.65$), for 'Ōpae'ula, Poamoho, Kahanahāiki, and Palikea, respectively. Although the Poamoho relationship appears significant, removal of two extreme outliers changes the relationship ($R^2 = 4\%$, $p = 0.14$) to a similar level as recorded elsewhere. This implies that, for the most part, longer dispersal distances can be either single movements or

a sum of successive movements. Additionally, some short distances can be a sum of return movements or just a single movement.

Emigration Simulation and Dispersal Correction

Our simulations rested upon assumptions of non-preference for dispersal direction, independence of successive movements, and equal potential for dispersal from any point within the site. We tested preference for one or more directions of movement using the Rayleigh test (Zar, 1984), in which the null hypothesis is no preference for directionality. Random directionality was confirmed at 'Ōpae'ula (61

TABLE 2. Uncorrected monthly survival rates, age-specific where available, with associated standard errors (SE) and 95% confidence intervals (LCI - lower 95% boundary, UCI - upper 95% boundary). Corrected rates, which account for emigration, are listed in the final columns. Means are percentages of population surviving per month. Annual survival is calculated by raising the mean monthly survival estimate to the 12th power; data were insufficient to support a model with varying survival among any age groupings at Poamoho and Palikea.

Species	Site	Age Class	Mean	SE	LCI	UCI	Annual Survival	Corrected Mean	Corrected Annual Survival
<i>Achatinella sowerbyana</i>	Poamoho	-	0.929	0.010	0.907	0.946	0.413	0.938	0.464
	'Ōpae'ula	Juvenile	0.941	0.021	0.831	0.981	0.482	0.934	0.441
		Subadult	0.983	0.011	0.935	0.995	0.814	0.987	0.854
		Adult	0.978	0.006	0.958	0.989	0.766	0.982	0.804
<i>Achatinella mustelina</i>	Palikea	-	0.942	0.011	0.915	0.96	0.488	0.956	0.583
	Kahanahāiki	Juvenile	0.901	0.019	0.819	0.948	0.286	0.891	0.250
		Non-juv	0.934	0.007	0.888	0.962	0.441	0.941	0.482

movements total, $p = 0.47$), Poamoho (30, $p = 0.62$), Kahanahāiki (15, $p = 0.87$), and Palikea (23, $p = 0.32$). It was uncommon to observe a snail dispersing more than once, so analyses of autocorrelation with regards to dispersal direction were not possible. We also found no association between any portion of a site and increased dispersal.

The probability of missing a dispersal event increased with distance of dispersal. During simulation of distances of 1–30 m from all points on the grids, shorter distances (1–3 m) remained within the grid as frequently as 90%. Longer distances in excess of 20 m ended up within the grid less than 10% of the time. To obtain the corrected dispersal distributions (Fig. 5), we simply divided the frequency of each observed dispersal distance by the frequency of detection on the grid during simulation. To illustrate, there were eight observations of 6-meter dispersal during field studies at 'Ōpae'ula, and 6-meter dispersal resulted in on-grid positions in 70% of simulations. Dividing 8 by 0.7 gives us the corrected frequency of ~ 11.

Provided that a dispersal event has occurred, the proportions of simulated dispersal events that end outside the study site boundaries are provided in Figure 6 for each origin point on the grid. These proportions were weighted by the frequency of occurrence, and then averaged to obtain a single proportion for each site. Average proportions were 0.394, 0.284, 0.354 and

0.494 for 'Ōpae'ula, Poamoho, Kahanahāiki, and Palikea, respectively.

To calculate emigration rates, we multiplied these proportions by our uncorrected dispersal rates, resulting in emigration rates of 0.067, 0.018, 0.007, and 0.046 in that same order. Corrected dispersal rates were obtained by adding emigration rates to our uncorrected dispersal rates, all of which are summarized in Table 3. Survival rates were corrected by running Program MARK with the emigration stratum, U . In most cases, this re-analysis significantly increased our estimates of survival (Table 2).

The two-day surveys in August 2008 provided adult abundance ($\pm$ standard error) estimates of 191 (± 20), 74 (± 16), 53 (± 4), and 25 (± 3) for 'Ōpae'ula, Poamoho, Kahanahāiki, and Palikea, respectively. The areas of each site (Fig. 2) were 550, 1388, 975, and 275 m², in that same order, corresponding to densities of 0.34, 0.05, 0.05, and 0.09 snails/m². We can use Palikea as a practical example of the translocation application by assuming an enclosure was to be erected around the site perimeter delineated in Figure 2. Abundance was estimated at 25 adult snails, and multiplying 25 by the emigration rate of 0.046, we get ~ 1 migrant per month. On an annual basis, this translates to 12 migrants per year to translocate from surrounding populations into the reserve, and vice versa.

DISCUSSION

Survival Rates

Age-class effects on survival were apparent for only Kahanahāiki and ‘Ōpae‘ula, although the other sites probably follow the same trend (Hadfield et al., 1993). Very few juvenile snails were recaptured at Poamoho and Palikea, so those survival estimates reflect mostly the adult individuals. Annual survival rates at Kahanahāiki (before accounting for emigration, Table 2) closely matched the estimates of Hadfield et al. (1993), which were obtained from a conspecific population located 200 m away. This further strengthened confidence in using our new methods to estimate survival at other sites.

Juvenile survival was, as in Hadfield et al. (1993), found to be nearly half that of the non-juvenile survival rates when comparison was appropriate (Table 2). Survival was clearly highest for all age groups at ‘Ōpae‘ula. Not coincidentally, this is also the only site where the predatory snail *Euglandina rosea* has yet to be seen. Rats and *E. rosea* are both present at the other three sites, and survivorship is similar among

them. These data suggest that predator control efforts should be increased at these three sites, until survival rates approach levels at ‘Ōpae‘ula. Survival rates did not significantly vary with time at any site, supporting the notion that massive predator influxes (as in Hadfield et al., 1993) did not occur during our study, but rather that predation pressure may be constant.

Recapture Rates

As expected, both Palikea and ‘Ōpae‘ula showed increased recapture probabilities in previously flagged trees, which is evident by the $p(s)$ parameters in both sites’ top models (Table 1). Kahanahāiki did not reveal this same pattern, probably because most trees were flagged early in the study, leaving few data available to estimate any un-flagged tree parameters. It was not surprising that Poamoho also did not show this pattern; flagging is quickly destroyed by the constant and fierce winds to which that site is exposed. Detection probability increases among larger age-classes were intuitive, as were increases due to increased search effort.

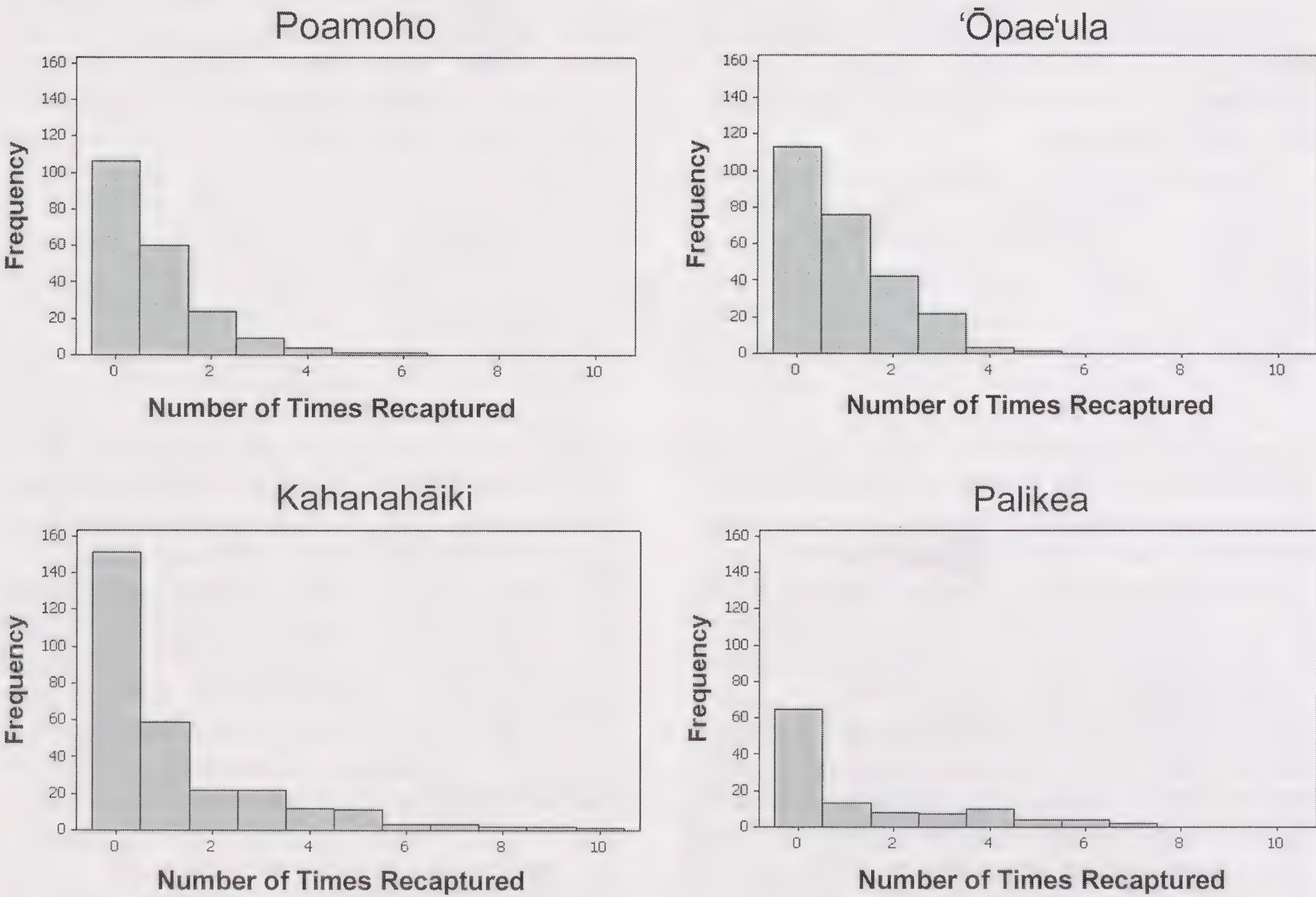


FIG. 4. Histogram showing the frequency of snails being recaptured X number of times at each site (*A. sowerbyana* – top panels, *A. mustelina* – bottom panels).

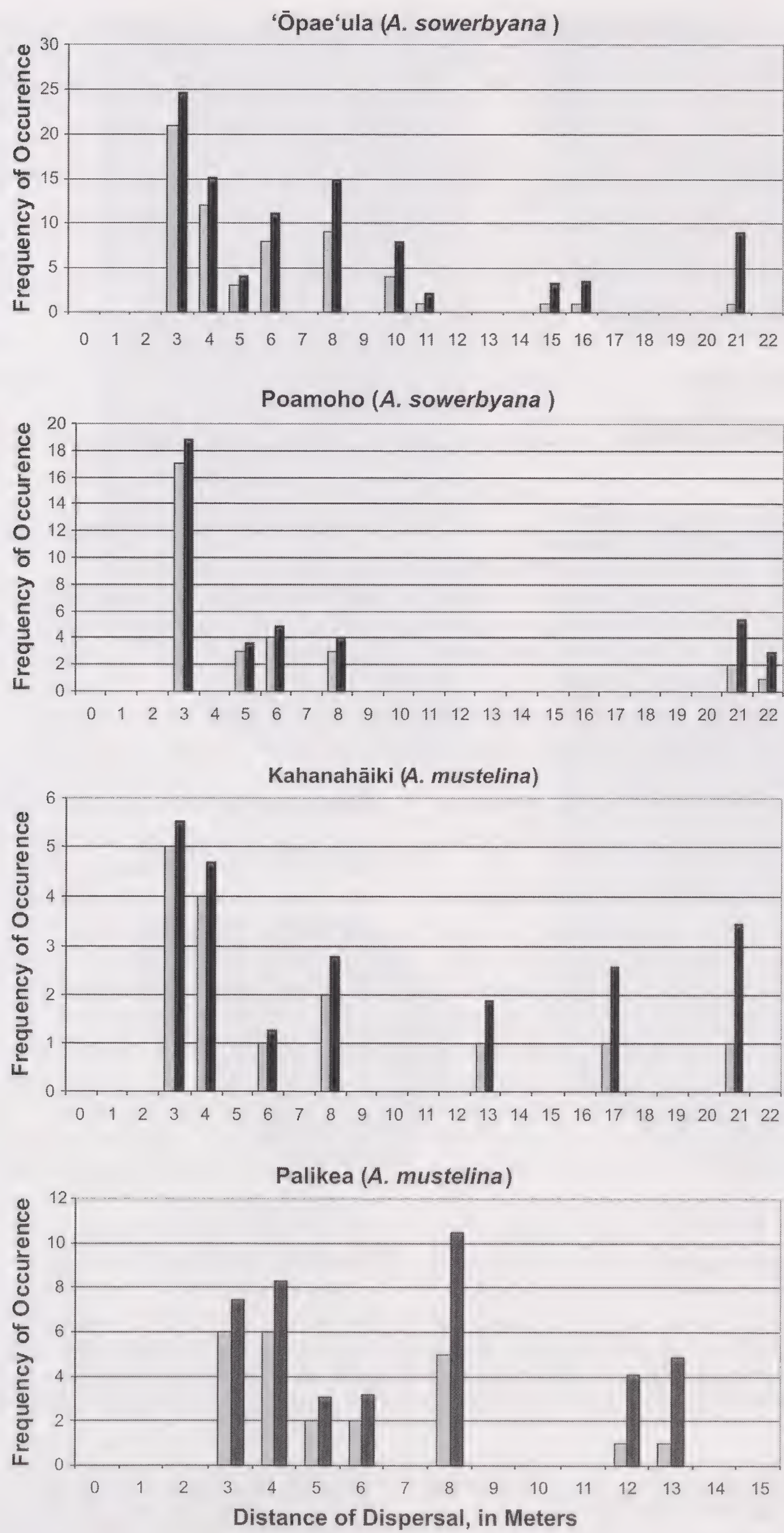


FIG. 5. Uncorrected and corrected distributions of snail dispersal distances, by site, from 2005 through 2008. Gray bars indicate the actual frequency of observed dispersal distances (uncorrected). Black bars represent the results of simulations, which include non-observable emigration (corrected).

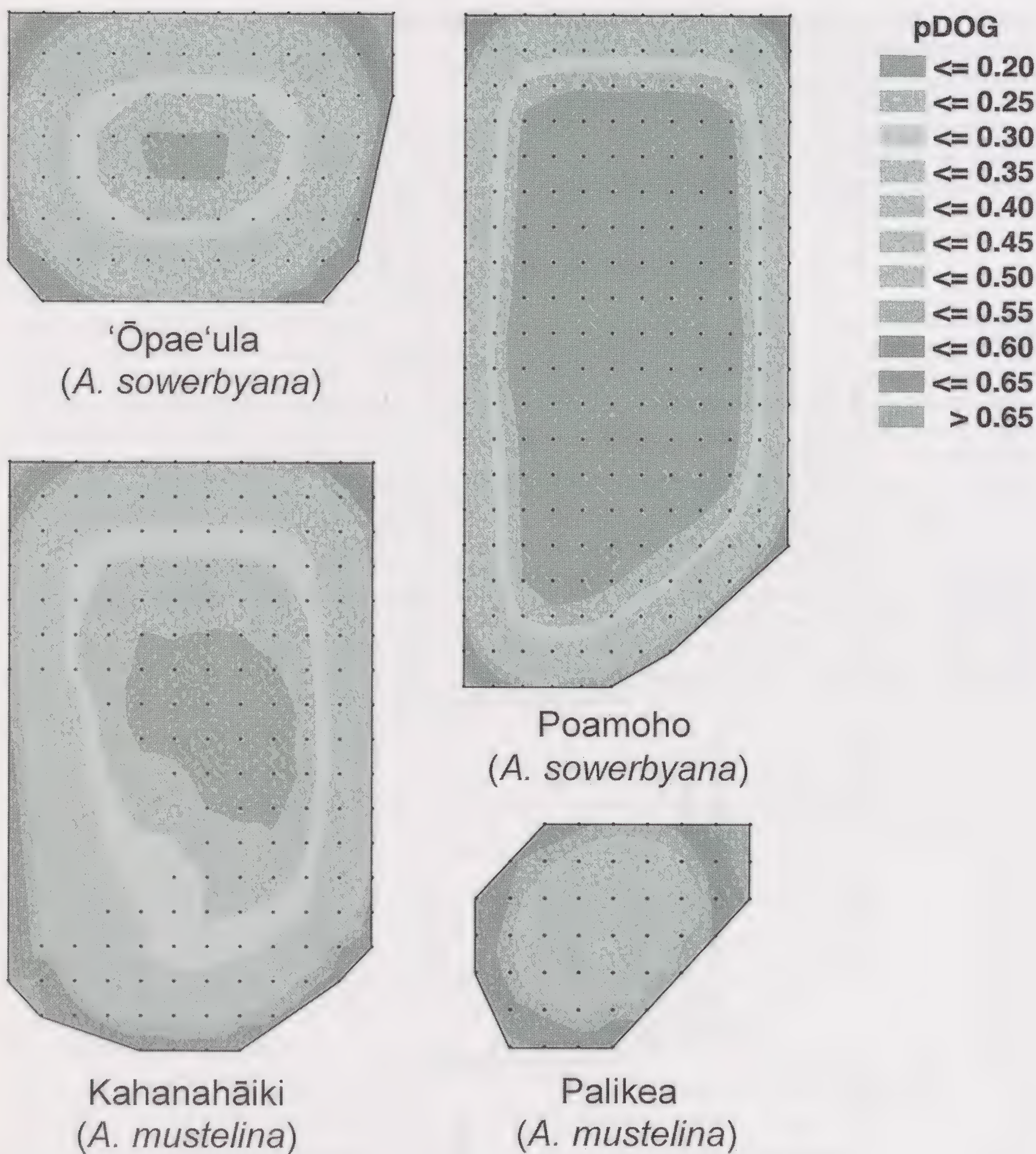


FIG. 6. Probability that random-direction dispersal events, sampled from simulated distributions of distances at all points on the grid, will end up beyond the boundaries of the study sites. pDOG is the probability of dispersal off-grid; lower values of pDOG are found in the center of the site.

Recapture proportions (Fig. 4) reflected the relative exposure of each site to inclement weather. In decreasing order from least exposure to greatest are Kahanahāiki, Palikea, Opae'ula, and Poamoho (Hall & Hadfield, 2009). The two lowest recapture proportions were both from *A. sowerbyana*, which occurs in the Ko'olau Mountains where wind

speeds are more extreme. This pattern was not surprising because dispersal and emigration are increased in areas of high wind (Hall & Hadfield, 2009), and surveys are difficult in areas with severe weather. In contrast, many *A. mustelina* were recaptured multiple times at the two Wai'anae sites (Fig. 4) where weather conditions are more benign.

TABLE 3. Summary of emigration and dispersal rates at all four sites. Corrected dispersal rates are calculated by adding uncorrected dispersal rates to emigration rates, which are themselves a product of off-site proportions and uncorrected dispersal rates. Parentheses for Poamoho rates indicate the increased rates from the December 2007 storm.

Species	Site	Uncorrected dispersal rate	Off-site proportion	Emigration rate	Corrected Dispersal rate
<i>Achatinella sowerbyana</i>	Poamoho	0.063(0.119)	0.284	0.018	0.081(0.137)
	‘Ōpae‘ula	0.169	0.394	0.067	0.236
<i>Achatinella mustelina</i>	Palikea	0.093	0.494	0.046	0.193
	Kahanahāiki	0.020	0.354	0.007	0.027

Dispersal Rates and Distances

Transition probabilities did not differ among age groups, but again, this could be because of low recapture rates of juveniles (and even fewer records of juvenile movement). All sites showed some effect from the December 2007 storm in at least the 2nd best model, and Poamoho showed a substantial increase in dispersal following the storm in its top model. Poamoho is exposed to winds far more than any other site (Hall & Hadfield, 2009), which may provide an explanation as to why only this one site revealed such a strong effect. Long-term weather records (United States Weather Bureau, 2008) will further assist conservation managers in guiding episodic translocation rates for this population, based on the frequency of severe storms.

‘Ōpae‘ula had a substantially higher rate of dispersal than any other site, possibly due to its exposure to both easterly and westerly wind gusts along an exposed Ko‘olau ridge. Poamoho has even more extreme exposure to NE trade-wind gusts, so it is unclear why ‘Ōpae‘ula would show higher rates. Kahanahāiki had a significantly lower rate of dispersal than all other sites, possibly because of its dense, tall vegetation (Cowie, 1980) and location being set back from an exposed ridge. Wind speeds have been recorded at all sites and Kahanahāiki was consistently the calmest (Hall & Hadfield, 2009). Palikea and Poamoho (not including the December 2007 effect) had nearly identical dispersal rates, and have similar ridgeline locations. There does not appear to be a species effect on dispersal rates, which seem to be dependent primarily on site location and exposure to inclement weather.

The dispersal estimates of this study are in close agreement with preliminary estimates obtained using radar tracking techniques (Hall & Hadfield, 2009). In that study, monthly dispersal rate estimates were 0–20%, which is similar to the 3–24% in this study (Table 3). Radar tracking also revealed an average monthly dispersal distance of 4.94 m, similar to that observed using CMR (5.25, 5.50, 6.39 and 5.12 m for ‘Ōpae‘ula, Poamoho, Kahanahāiki, and Palikea, respectively, Fig. 5).

Management Implications

To mimic natural gene flow across reserve boundaries, we recommend a rate of exchange between neighboring populations analogous to simulated emigration rates corresponding to relevant reserve dimensions. This rate should be equal for the number of adults moved both into a reserve and out of the reserve. The tree snail system provides a simplistic example with which to illustrate this approach, owing to the species’ short dispersal range and small reserve (exclosure fence) sizes. Our proposed methods should require minimal modification for use with larger and more vagile species in larger reserves, where rather than fences, reserve boundaries might be roads or other inhospitable landscapes.

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